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by

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Phylogenetic Footprints in Organizational Behavior *)

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Abstract
An evolutionary tool kit is applied in this paper to explain how innate social behavior traits evolved in early human groups. These traits were adapted to the particular production requirements of the group in human phylogeny. They shaped the group members' attitudes towards contributing to the group's goals and towards other group members. We argue that these attitudes are still present in modern humans and leave their "phylogenetic footprints" also in present-day organizational life. We discuss the implications of this hypothesis for problems arising in firm organizations in relation to the coordination and motivation of organization members.

Key Words: evolution, pre-adaptations, group selection, firm organization, organizational behavior, leadership

JEL Codes: B25, D03, D23, D74, M14

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1. Introduction

According to a popular metaphor, firm organizations are like organisms. They have a life distinct from, but not independent of, that of their members. They develop in the course of time like natural organisms do, perhaps even analogously to their life cycle (Marshall, 1920, Book IV, Chap. 12 and 13; Penrose, 1959; Quinn and Cameron, 1983). However, biology may have more to say on organizations than is apparent in such metaphors and analogies. In the light of recent biological research on the evolution of social behavior, firm organizations and human groups more generally can be seen as yet another outcome of social evolution. In nature, social evolution has brought forth super-organisms like colonial invertebrates, e.g. social insects, and some social mammals (Hölldobler and Wilson, 2008; O'Riain and Faulkes, 2008; Seeley, 2010). Similar to members of these biological super-organisms, the social behavior of members of human organizations is also influenced by traits that are part of their genetic endowment. These traits have been shaped through natural selection forces during the species' phylogeny (Alexander, 1974; Wilson 2012).

In the case of the members of the afore mentioned super-organisms, this influence is very strong because their phenotypic plasticity is usually very limited. Modern humans, in contrast, show a great deal of plasticity. They adjust their social behavior by reinforcement and conditioning learning as animals do, albeit in a form that is much more culturally differentiated. The largest difference is, however, in their capacity to adjust by cognitive and social learning. The influence of inherited behavior traits is therefore more indirect and subject to extensive cultural mediation. Nonetheless, it is still there and affects the way in which organizations function.

Every generation of humans is genetically endowed with basically the same emotional and cognitive apparatus with which our ancestors were already endowed. Since modifications resulting from natural selection forces are, in relation to human time scales, extremely slow, the inherited social behavior traits are most likely not much different from those of our early ancestors. Yet, the adaptive value which these traits had at those times is not necessarily present any longer under the dramatically different living conditions of today. Genetic pre-adaptations suitable to life in early human groups do not necessarily match well with the requirements of modern social life, particularly in organizations (on other cases of mismatch, see Burnham 2013 in this issue). Indeed, by recourse to hypotheses from sociobiology and evolutionary psychology,

recent research in organization science has already identified several effects of pre-adaptations on social behavior. Gender-specific pre-adaptations seem to be behind such phenomena as occupational segregation (Browne, 2006) and status segregation (Colarelli, Spranger and Hechanova, 2006). Organizational citizenship behavior may be due to pre-adapted behavior that signals individual superiority according to the handicap principle discussed in biology (Deutsch Salomon and Deutsch, 2006). Furthermore, leadership-followership behavior in organizations and beyond may be attributed to pre-adaptations (Van Vugt, Hogan and Kaiser, 2008; Van Vugt and Ahuja, 2010).

In a similar spirit, the present paper explores the importance of what we dub the "phylogenetic footprints" in organizational behavior in relation to the core problem of coordination and motivation. This dual problem is well known from the theory of the firm (see, e.g., Witt, 2005). It actually arises, however, wherever groups of humans (or non-humans) jointly engage in productive activities. If social behavior falls short of what is necessary to solve the dual problem, groups of individuals are unlikely to gain an advantage by forming a group. Regarding human organizations, the question is how social behavior traits that have been inherited from our ancestors affect coordination and motivation today.

To answer this question, we need to be more specific with respect to what the relevant traits are. Accordingly, we draw on research from evolutionary anthropology (Boehm, 1989, 2001, 2012) and ethology (Eibl-Eibesfeldt, 1970). Eibl-Eibesfeldt argues that different social behavior traits such as the selfish dispositions and the pro-social dispositions conflicting with the former, most likely originated from different phylogenetic stages. There is a legacy of our primate ancestors with their opportunistic and agonistic behavior towards their con-specifics (Eibl-Eibesfeld, 1997, 525-560). Yet, there is also the legacy from early hominids and Homo sapiens with their – phylogenetically more recent – adaptations to living in groups (Boehm, 2001, 1989; Campbell, 1965; Erdahl and Whiten, 1994; Masters, 1989). These adaptations ensured degrees of coordination and motivation that, on average, brought individuals a selection advantage from forming, and cooperating within, groups.

From an economic point of view, an important condition to prevail in group competition is internal coherence. In the huge literature on group selection, this condition is interpreted mostly as a problem of motivational coherence. If group members cannot be motivated to share, help, and contribute to group goals at an adequate level of effort, individual interests such as

effort minimization or exploitation of group resources would gain priority over those of the group. Motivational coherence thus requires that free riding, agonistic and, anti-social inclinations are kept in check within the group (Wilson 2012). However, internal coherence also requires a reasonable degree of coordination in the group members' actions. Pro-social motivation alone does not ensure that the group members' activities are indeed coordinated with regard to the group's common goals. If that coordination fails, inner-group malfunctioning and frictions might spoil group action or even cause break down.

Multiple coherence requirements are thus expected to be a recurrent theme of life in groups from the early hominids to the modern organization. An understanding of the role of "phylogenetic footprints" in organizational behavior can help to improve and stabilize organizations, particularly if put in perspective with the different ways in which groups have tried to account for these requirements in human history. To make this point we proceed as follows in the remaining parts of the paper. Section 2 lays out in more detail the dual problem of coordination and motivation within groups. We draw on Wilson and Gowdy's (2013 in this issue) "evolutionary tool kit" to explain why we use an evolutionary approach and how it helps to structure our search for "phylogenetic footprints" in organizations. Section 3 highlights the conditions under which the social behavior traits, today virulent as behavioral pre-adaptations, most likely evolved in early human groups. We discuss how coordination and motivation problems can be conjectured to have been solved in these groups. Section 4 argues that technological and institutional changes later triggered an increase in group size. We explain why, under the new conditions, a very different solution of the dual problem emerged in a cultural adaptation process. In Section 5, we turn to modern organizations (if not otherwise stated: firm organizations). We discuss what role "phylogenetic footprints" play for understanding the basic mechanisms of coordination and motivation. Referring to the previously identified influence of group size we finally address in Section 6 the effects of organizational growth on the conditions for solving the dual problem. Section 7 concludes.

2. The role of coordination and motivation for group success

All species need to produce and consume what is necessary to support their subsistence, i.e. to maintain their metabolism, and to reproduce. In some species, this is accomplished by

solitary action, in others through the socially organized actions of the members of a group. Homo sapiens is a social species. Why did humans develop a socially organized form of production in their early phylogeny, and why did innate behavior traits evolve in humans that supported this form? In terms of Wilson and Gowdy's (2013) "evolutionary tool kit", this is the question of the ultimate cause for human sociality, i.e. human dependence on living and producing in groups. The answer is, it seems, that hominids managed to better acquire and protect food sources, most notably high protein meat, and to reproduce more successfully when forming groups and keeping them together (Gintis, 2013; Hrdy 1999; Stiner, Barkai and Gopher, 2002). Reliable cooperation among group members most likely also improved protection against predators and rivals, reduced some of the risks of living such as starvation, supported child rearing, and raised individual productivity by allowing a division of labor and specialization in hunting, gathering, shelter provision, and food preparation. All these effects were to the advantage of the entire group and, thus, the average group member.

However, a group's capacity to realize productivity gains depends on how well the division of labor and specialization function within the group. This is the dual problem already mentioned in the introduction. First, within the group, specialized individual activities must be sufficiently coordinated. This means that the differentiated work inputs required by the utilized production technology need to be partitioned and assigned as tasks to group members. Furthermore, sufficient information and skills are necessary to enable the group members to actually deliver the assigned work inputs. Second, all division of labor and specialization presuppose mutuality in contributing to the group's production. The group's productive success not only depends on how well coordinated the individual activities are. It also depends on the degree to which free-riding on these productive activities is prevented. If free riding becomes endemic in the group, it is likely to paralyze the division of labor and specialization and, eventually, the group's very purpose of existence. Put differently, group members have to be motivated to a sufficient degree to take on, and identify themselves with, the tasks which have been bestowed upon them. Refraining from opportunism and free-riding is therefore an essential part of within-group cooperation. Other important, but economically less significant, parts are mutual support in reproducing and restricted use of personal violence against other group members.

In face of the ambivalent behavior traits of its members, a group's pro-social solution of the coordination and motivation problem always represents a delicate balance. Spontaneous coordination with, and intrinsically motivated support of, the group – instead of confusion, free-riding, and attempts at exploiting others – is likely to be upheld only as long as the group manages to maintain a spirit of group coherence against the agonistic tendencies of its group members. Group selection may have favored groups whose members happened to display above-average pro-social behavior traits, thus establishing a relative reproductive advantage for such traits (Sober and Wilson, 1998; Wilson, 2011; Wilson and Wilson, 2007). Co-evolution of pro-social genetic dispositions and group-specific, culturally acquired, patterns of keeping confused, selfish, and agonistic behavior in check are also likely to have been important for stabilizing this delicate balance (Richerson and Boyd, 2005). Thus, we claim that sufficient degrees of within-group coordination and motivation are ultimately a crucial economic contingency for groups to have a selective advantage in group competition, no matter whether concerning small bands of hunter–gatherers, "groups" of market participants, or organization members interacting more or less anonymously on a contractual basis.

How is production functionally organized so as to accomplish sufficient degrees of coordination and motivation? This is a question that can usefully be distinguished from the question of why production is socially organized. In terms of Wilson and Gowdy's evolutionary toolkit, this question pertains to the proximate causation of the particular form in which production is organized. The answer varies for different times and places. Hunter-gatherer bands differ dramatically from feudal fiefdoms or modern firm organizations regarding the "mechanism" of coordination and motivation and, in particular, how free-riding is suppressed. However, later "mechanisms" of solving the coordination and motivation problem have emerged from earlier ones. To draw on yet another tool from the tool box, a study of the evolutionary history which connects these very different forms of productive groups can generate important insights into how the mechanisms were adapted in a cultural, evolutionary process.

In this process, newly created military and productive opportunities and, as can be conjectured, changing beliefs and world views create conditions for trying new mechanisms of coordination and motivation. On the other hand, the behavioral pre-adaptations inherited from the early human phylogeny (adapted to the living conditions of productive groups at those times) remain as constraints. Since they also influence behavior at later stages, they imply natural

constraints on the mechanisms of coordination and motivation that be become feasible at later stages. Given the space limitations in this paper, we confine our discussion to two functionally different types of mechanisms by which coordination and motivation have historically been accomplished. These two mechanisms exist in more or less modified form to the present day. As discussed further below, these mechanisms can also be found in modern firm organizations which, after all, are more or less coherently acting groups pursuing a productive purpose. These groups still have to cope with the ambivalence of the behavioral pre-adaptations of their members.

3. Social behavior, coordination and motivation in early human groups

There is plenty of evidence that ancestral social life has taken place in small, band-like structures composed of a size from a few dozen members up to 150 members.[1] The nucleus of human sociality that gave rise to these band-like structures can be conjectured to be the emotional tie between mother and child (Eibl-Eibesfeldt, 1997). It is the main origin of pro-social emotions and caring behavior, and our common mammalian heritage. A specifically human characteristic, Eibl-Eibesfeldt (1997, 322-326) claims, is the extension of the dyadic mother-child relationship in the early hominids to a triad by inclusion of the father. During the formation of this triad, several behavioral and emotional patterns, formerly exclusive to mother-child relationship, were transferred to the mother-father relation (e.g. courtship, sexual behavior) or the father-child relation (caring behavior). This finding is supported by various anthropological studies showing a strong emotional father-child relationship across cultures which is much stronger in humans than in all other primates. The relationship can be extended to also include female relatives, grandparents, and band members more generally.[2]

[1] Boehm (2001). Similar patterns can still be observed in hunter-gatherer communities living today. Exploring their group size, Marlowe (2005) found an average size of 48 group members (median 30) based on a sample size of 294 groups. Evidence from neuroscience supports the view that the maximum stable group size of local bands is around 150 members (Dunbar, 1993; Eibl-Eibesfeldt, 1997, 410-415).

[2] See Hrdy (1999). In early humans, the extension seems to have been limited to members of one's own small group. The limitation corresponds to an antagonistic emotional attitude towards con-specifics. On the one hand, humans have pro-social needs that cause them to seek the proximity of others. On the other hand, an encounter with less familiar con-specifics often

Judging by the conditions of their present-day hunter-gatherer correlates, the early bands or local groups were relatively stable social units that occupied and defended a certain territory. The genetic relatedness across the groups may have been lower than often supposed (Hill et al. 2011). Over the long period in human phylogeny during which interactions were organized in these small groups, it is likely that genetic behavior traits in the group members co-evolved with a learning process of cultural rules that established social constraints on behavior (Boyd and Richerson, 1982). Competition between groups and group selection is likely to have favored particular behavioral dispositions and cultural rules, namely everything improving the coordination of the group members and motivating them to contribute to the productive needs of the group enhanced survival and reproduction chances for all group members (Bell et al., 2009). But, as mentioned, there are also behavioral dispositions not conducive to group cohesion. Like almost all social animals, humans can also show selfish behavior: free-riding, aggression in competing with other group members for resources and status, attempts to manipulate, deceive, and exploit others, and so on. Such behavior can be traced back to our primate ancestors (Eibl-Eibesfeldt, 1997, 525-560) where it was instrumental in gaining an advantage in accessing mating partners, food sources, or other resources (as it can still be today).

The ambivalence of social behavior also shows up in the status distribution within groups. At one extreme, there can be an egalitarian order. At the other, a strictly enforced hierarchical dominance order is possible. Suppressive dominance hierarchies are common among many social animals, but are not necessarily very stable. We know from observations of our closest relatives - the chimpanzees - that they developed a social system which is based on strict dominance orders.[3] The primate ancestors of the hominids may have had a similar social structure. It is then likely that the early humans inherited behavioral dispositions which pre-programmed an emotional ambivalence in them (Boehm, 1989; Erdahl and Whiten, 1994; Masters, 1989; Sober and Wilson, 1998).There is a more or less strong disposition to dominate,

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triggers shyness, fear, or even aggressive behavior. The in-group/ out-group antagonism that is implied here tends to strengthen cohesion within the own group. For a discussion see Berreby (2005).

[3] See Riss and Goodall (1977). These hierarchies are usually enforced by physical dominance. The alpha animal has privileged access to resources and mating partners. Lower ranked animals are constrained in these respects. They often turn into rivals, particularly young adult animals and immigrants. The alpha animal then has to defend its status by threats and physical violence, thus incurring substantial health and survival risks.

i.e. to enjoy a high position in a social hierarchy (expecting submissive behavior on the part of lower ranked persons). But there is also a deep-rooted fear to fall behind in status and become victim of a dominance order invoked by others.

In his seminal work combining anthropological and paleo-archeological studies with theoretical evolutionary arguments, Boehm (1993, 2001, 2012) has tried to reconstruct the social system of our Pleistocene ancestors. Starting from the observation that the vast majority of indigenous societies living in bands today are characterized by a strongly egalitarian structure, he argues that egalitarianism and the rejection of strong dominance hierarchies is a basic attribute of human sociality. With their growing cognitive abilities, early humans may have realized that, if not able to themselves dominate, it would be best to also prevent others from doing so. This rising intelligence made strategic thinking, proto-political finessing, and coalition-seeking behavior feasible. Through use of such faculties, dominance striving can collectively be tamed wherever attempted by strong group members.

The means of blocking dominance ambitions, Boehm claims, were macro-coalitions which the weaker group members formed. In contrast to despotic, repressive dominance structures where one alpha individual dominates all others, the coalition itself takes the position of a dominator ("reverse dominance hierarchy", Boehm, 2001). Several “intentional leveling mechanisms” have been observed by which groups are able to enforce the egalitarian ethos they promote.[4] Desertion and/or group fissioning are the most drastic examples. Thereby, either the whole group leaves the leader or the group divides into two or more. By reducing the size of the group, the coordination of the remaining individuals again becomes easier. Over thousands of generations in early human phylogeny, a more or less strong emotional disposition for living in a

[4] In a survey analyzing 48 small primordial societies, partly organized as egalitarian hunter-gatherers, partly as chiefdoms, Boehm (1993) reports regular intentional sanctions placed on leaders who overstepped their prerogatives or individuals trying to usurp the group such as public opinion and open discussion in councils, criticism and ridicule, and open disobedience. In more severe cases, the egalitarian alliance also ostracized the leader and terminated his leadership. In some cases, the African !Kung, the Australian aborigines, and the south American Yaruro even executed former leaders or “extremely aggressive men”. Bingham (1999) has speculated that the threat of being injured by stone-throwing – a technique that must at some time have been invented in human phylogeny – may have been instrumental in guaranteeing a balance of power within the early groups.

society of equals may have emerged.[5] It continues to exist with the earlier, dominance-oriented dispositions toward social behavior. (Some social skills in arranging/switching coalitions may also have entered the genetic endowment.)

The early human groups survived and reproduced quite successfully. It can therefore be inferred that, despite their ambivalent social behavior traits, they were able to sufficiently coordinate and motivate their members vis-à-vis the productive challenges they faced. By what specific "mechanism" did these groups accomplish an apparently quite effective coordination and motivation (the question of proximate causation of an emerging social arrangement)? In the absence of a strong dominance order, a group of dozens of more or less equal individuals can come up with a multiplicity of individual ideas and plans about what needs to be done when and by whom. These ideas may often be incompatible or even conflicting ones. Coordinating such a group toward a joint pursuit of productive purposes requires a mechanism that aligns plans, resolves conflicts of interest, and reaches agreement about what tasks are assigned to whom. Given that the hunter-gatherer production technology requires a rather low daily working time per capita (Werner et al., 1979), it can be imagined that there was enough time left to engage in palavers and negotiations. Under such conditions, it is likely that a mechanism of coordination emerged spontaneously that promoted consensual decisions and voluntary agreements within the group. Successful earlier interactions and coordination devices may have evolved into group specific traditions, perhaps even customs.

It is conceivable, however, that urgent new tasks required more rapid forms of coordination, particularly in case of threats and crises. In such cases, pro-social leadership, based on persuasion rather than dominance, can facilitate the coordination of a group by, for example, influencing the agenda of intra-group communication and mediating compromises in case of intra-group conflicts. An egalitarian structure does not necessarily exclude that such leadership can arise from someone's overriding social skills, charisma, and/or capabilities and experience.[6]

[5] Evidence for this disposition has recently also been provided in experimental studies of the dictator game in hunter-gatherers, see Henrich et al. (2004).

[6] Leadership of this kind is more akin to a "primus inter pares" relationship as discussed in Boehm (1993). In human ethology several forms of dominance relationships are distinguished such as a “caring dominance” (characteristic of the parent-child relationship), a repressive dominance order, and what is called “pro-social dominance”. The latter is a uniquely human form based on superior leadership competencies. It is frequent in groups in which the members are very familiar with one another (Eibl-Eibesfeldt, 1997, 424).

Once proven to enhance coordination, regular reliance on such pro-social leadership may have fostered an advantage in group competition and, hence, been selected for. This is even more true whenever informal leadership is instrumental in organizing support for needy group members and/or reducing efficiency losses through more coherent assignment of tasks.

With respect to the mechanism by which group members are motivated to contribute to the productive purpose of the group, an egalitarian group structure is an important proviso. It is known to elicit a higher identification with the group and a pro-social attitude. This, in turn, tends to raise the commitment of the group members to pursue an assigned task, particularly if the assignment is based on a consensus. An intrinsic work motivation is created, i.e. an attitude for which accomplishing the assigned tasks is a major element of reward (on intrinsic motivation, see Deci and Ryan 1985). Nonetheless, the mentioned ambivalence of behavior traits regarding selfish motives is a permanent threat to the motivational mechanism on which egalitarian groups rely.

Since the productive performance of a group is vulnerable to free riding and agonistic behavior on the part of its members, such tendencies need to be kept in check. To some extent, reproductive groups can tame tendencies in this direction during the socialization processes. Similar to how self-control of sexual drives is a matter of education, education can raise self-control of these agonistic dispositions. The mere fact that both can be instinctive and innate does not imply that they cannot be channeled into more sublime forms of conduct that are less destructive for groups. However, this may not always work. Effectively monitoring and sanctioning free riding is therefore indispensible.[7] Because of the intense interaction and communication between their members, small groups seem to have an advantage in this respect. They also seem to better be able to activate moral aggression and social ostracism against free riders, particularly where this is costly to those engaging in punishment behavior. To keep up a regime in which individual behavior that undermines group cohesion is sanctioned, the collective provision of a public good is required. As is well known, this tends to be more difficult to

[7] ocial sanctions are necessary and can indeed often be observed in present day hunter-gatherer societies (Bernhard, Fehr and Fischbacher, 2006; Boehm, 2012, 179; Boyd and Richerson, 1992; Fehr and Gächter, 2000; Witt, 2008). Without them, selfish behavior would be more rewarding than non-selfish behavior. Sooner or later, it would be imitated, proliferate in the group, and eventually undermine the group's cohesion and, consequently, its selection advantage.

accomplish, the larger a group becomes and/or the more frequently costly sanctioning activities are necessary. Informal, pro-social leadership (e.g. opinion leadership) may facilitate the organization of the collective action and encourage moral aggression. It cannot, however, eliminate the costs that are quickly increasing as groups grow larger. The ambivalence of human social behavior traits can therefore be expected to challenge the motivational mechanism of egalitarian groups, as well as their productivity, as group size increases. As will be discussed in the next section, other mechanisms of coordination and motivation may then turn out to be favored by group competition.

4. Dominance-based mechanisms of coordination and motivation

The innate social behavior traits that had been shaped by natural selection during the long epoch of early human evolution continued to be present in the genetic endowment when, over the last ten to fifteen thousand years, human sociality was transformed further. Given the slow pace of genetic evolution, these transformations have been the almost exclusive result of cultural evolution, i.e. of (collective) learning, formation of habits and customs, and changing constraints on social interactions. The significance of this period lies in the radical changes in the dominant production technology from that of the hunter-gatherers to agriculture. Correspondingly, the mechanisms of coordinating and motivating productive efforts also changed.

What exactly triggered the transition to agriculture and a more sedentary life style is difficult to reconstruct. Presumably, a number of factors have been influential (Price and Bar-Yosef 2011). Some of these factors must have forced the human groups then existing to abandon their reliance on hunting and gathering in order to achieve subsistence. The new, agricultural technology was initially quite precarious, delivering a lower supply of calories (Bowles 2011), while necessitating longer and harder work and causing a deteriorating health standard (Cohen and Crane-Kramer 2007; Larsen 2006). A plausible, though not easy to prove, explanation for the adoption of the initially inferior new technology is the growth of the human population (Boserup, 1965; Cohen, 1977). The extensive, nomadic land use of foraging hunter-gatherers depends on the availability of uncontested land reserves with a sufficiently large biomass that can periodically be visited. With a growing overall population size, such land reserves become increasingly scarce. Previously nomadic groups may therefore have been constrained in their

foraging range with the result of an increasing over-exploitation of their local hunting and gathering resources. To compensate for their exhaustion, hunter-gatherer groups may eventually have been forced to settle down and start cultivating arable land, sowing, harvesting, as well as raising domesticated livestock.

Another consequence of increasingly scarce land reserves is a constraint on the social dynamics of growing groups or bands. If unoccupied land is lacking, it becomes difficult, if not impossible, for groups that grow large to fission and migrate into a separate territory. It can be conjectured that the former hunter-gatherer bands were thus prevented from maintaining their formerly rather small size. Beyond a certain size, however, the ability of a group to spontaneously form blocking coalitions is seriously hampered. Without blocking macro coalitions which, according to Boehm (2011), set limits to the dominance striving of single group members, an egalitarian group structure is difficult to defend.

In this context, a new economic property of agricultural technology is relevant: it requires substantial investment in, and accumulation of, productive resources. The accumulation of these resources demands effort and sacrifices by the individuals. Both can be expected to occur only if the fruits of such investment can sufficiently be secured against theft or robbery. Unlike in the case of hunter-gatherer groups,[8] agricultural production made it necessary to create extended possession titles and to enforce them effectively. However, once possession in livestock, seeds, harvested stock, and dwellings is protected, wealth can be accumulated and be used to support claims to a superior status. This is likely to have facilitated attempts of individuals or families within groups to gain a position of leadership. Accumulated wealth can be instrumentalized to buy allies, thereby undermining any remaining "reverse dominance hierarchies". Once other group members can be subdued and their productive efforts be exploited, leadership takes on a different character. Leaders then have an incentive to protect the source of the exploitative rent against external rivals and suppress internal opponents.

It has already been argued by Fried (1967) and Harner (1970) that the conditions of the new production technology favored the emergence of a hierarchically stratified society. This development began with the figure of the *locum tenens*, progressed with the delegation of power

[8] These groups had little to defend. They seem to have known only personal possession in portable tools and belongings. In case of loss, e.g. in inter-tribal fighting, they therefore suffered comparatively little losses in wealth.

in the form of governorship and fiefdom, and eventually unfolded into feudal state systems (Jones, 1993). The characteristic, new social relationship was therefore a vertical one between dominating individuals and their subordinates, i.e. between unequals.[9] Dominance and submission were characteristics of the social interactions of our primate ancestors, a pattern that had been overcome by the egalitarian hunter-gatherer groups, and now re-emerged. Egalitarian sentiments still present as part of the genetic endowment of those who now found themselves in a subordinate position must, by necessity, have been frustrated. This may explain the frequent violent upheavals against the ruling hierarchy and the dominators' use of draconian, public punishment of insurgents to deter and suppress such sentiments. The more subtle way of cementing hierarchical dominance was, however, to make subordinates believe that domination *and* submission are the "natural" or "God-given" model of social behavior.[10] Once subordinates accept such a model of social behavior, they may be prevented from even thinking of contesting the dominating position. Moreover, domination and submission are then likely to become the template of behavior at each layer in an unfolding domination hierarchy.

With the use of the agricultural technology, competition for survival was no less an issue than in the times of the hunter-gatherer technology. In fact, a new dimension of competition was even added: competitive growth. The limitations on both accumulation and group size characteristic of hunter-gatherers were relaxed. However, human sociality continued to take place in productive groups, albeit increasingly hierarchically structured ones. Hence advantages in group competition continued to matter, but became more complex as a result of the hierarchical stratification. Productive units at the same level of the hierarchy competed with one another, as did (coalitions of) units across the different levels. In any case, the greater the resources controlled, the greater the advantage in terms of political and military power. Greater resources also enabled group growth by allowing higher reproduction rates, gains from migration, and a subjugation of other groups. The amount of resources commanded was not least

[9] In a hierarchically stratified society, being on equal terms like in egalitarian hunter-gatherer groups is only possible, if at all, at the same layer of the hierarchy. But, at the higher ranks of the hierarchy, individuals at same layer have rarely formed a cohesive group. Their relationships were more often those of rivals than of allies.

[10] Supremacy was often tried to be legitimized with reference to real or pretended achievements, e.g. in warfare, or claims to divine status by the ruler. For a detailed discussion of the role of religion for social coordination in large groups, see Wilson (2002).

a function of the productivity of land use in the size of the controlled territory. Hence, the effectiveness of the mechanisms of coordination and motivation was a determinant of success in group competition in agricultural societies as well. Competition can manifest itself in the form of a group selection effect, if the culturally formed groups persist as stable units long enough. Yet, the preconditions for coordination and motivation in those extended groups, based on a hierarchical domination-submission relationship, are different from those of egalitarian hunter-gatherer groups. Competitive pressure to increase productivity fostered a different mechanism of coordination and motivation.

As far as coordination is concerned, a spontaneous consensus-oriented process of palavers and negotiations, such as the one practiced by the hunter and gatherers, remains, in principle, a possible default option. But this option is time consuming. Furthermore, this option is not known for producing very coherent of task assignments. A coordination mechanism in which orders are given by superiors to their subordinates – as it becomes feasible in hierarchical relationships – is more efficient in both respects. Moreover, the authority of superiors allows them to give orders in such a way that the group's activities are coherently focused on only one set of goals and plans – that of the superiors. Hierarchically governed groups coordinating production on the basis of such authority may therefore be able to make decisions faster and more coherently. However, this advantage translates into efficiency gains and a productivity advantage only if the group members can also be motivated to comply with the orders given to them and exert sufficient effort toward their execution. This refers to the motivational question that is the weak point of this governance regime.

Precisely because of the domination-submission relationship, a cooperative motivation is difficult to uphold or induce. The motivational mechanism of the hunter-gatherers groups benefits from the identification of their members with the group, a corresponding pro-social attitude, and the degree of self-determination they are allowed. It is well known that such a constellation induces a significant amount of intrinsic motivation toward productive activities (Deci and Ryan 1985). In a domination-submission relationship, in contrast, superiors who try to force their own production goals upon the subordinates in their group face a different situation, particularly if the legitimacy of their supreme status is contested. They usually resort to suppressive means to cement their dominance and can therefore not expect much identification with the productive purpose from their subordinates. Superiors of this sort cannot afford to leave

room for self-determined action and cannot count on intrinsic work motivation. The situation is pretty much that of a principal-agent relationship (Sappington, 1991): the principal has to motivate an agent to act on his behalf. The agent tries to withhold work effort, be it for opportunistic reasons or, in the times of ancient agricultural production technology, to prevent being physically destroyed by drudgery.

Indeed, for the most part of its history, agriculture required vast labor inputs, extremely long working hours, and, in particular, physically hard work. Agents cannot easily be motivated to do such work. Intrinsic motivation being absent, an almost exclusive reliance on extrinsic motivation is characteristic of the motivational mechanism. As in all principal-agent relationships, the principal tries to induce effort by recourse to the device of "carrot and sticks": paying the agent in kind for service delivered; utilizing crop sharing arrangements; but using physical violence against those withholding effort.[11] The obvious precondition for this motivational mechanism to work is an intensive monitoring of the agents' performance. This presents a dilemma. Weak or non-existent controls result in lower effort and, hence, lower productivity. Intense monitoring requires transferring significant human resources from productive to monitoring tasks. The larger the group, the more extended the hierarchy of controls. This subtracts from revenues accruing from land use. Moreover, as is known from the agency problem, where the principal cannot identify the agents' level of effort, or observe it independently of exogenous influences on their performance, effort cannot be made the basis for compensation. Under such conditions, extrinsically motivated agents tend to reduce their effort with corresponding productivity losses, except when threatened to be physically punished on a mere suspicion of withholding of effort.

From a modern point of view, many of the features of the motivating mechanism and the exploitative practices of historical agriculture appear cruel and unjust. It is likely, however, that they emerged under the competitive pressure within and among hierarchically stratified groups in pursuit of improving the productivity of land use (Gowdy and Krall 2013). The higher the productivity, however realized, the more resources could be controlled and instrumentalized for political and military competition. Where this relationship gave rise to selection advantages at

[11] The most suppressive form of dominance-based production is that of slavery. It has been present in almost all historical agricultural societies, see Drescher and Engerman (1998).

the group level, this provides be an example of cultural group selection not necessarily favoring groups with a cooperative, pro-social internal structure.

5. Old coordination and motivation mechanisms in new guise in modern organizations

In the preceding sections, two mechanisms of coordination and motivation have been highlighted. By reconstructing the historical conditions under which they emerged, we have tried to clarify why they fundamentally differ in how they function, i.e. in their proximate explanation. The first, informal and egalitarian mechanism reflects the specific production conditions of the hunter-gatherer economy and corresponds to innate social behavior traits that were selected for under those conditions. The second, dominance-based, hierarchical mechanism – the result of historically more recent cultural adaptations – reflects the very different production conditions of agriculture. Under these conditions, it was not possible to restrain the striving for dominance by some group members. Over the millennia a cultural tradition stabilized where a few superiors subjugated the many subordinates. This constellation implied not only a specific way of coordinating productive activities, but also of distributing both workloads and the produced output in a very uneven fashion. The second mechanism therefore conflicts with the egalitarian tendencies of humans and has adverse motivational effects. It has to rely on tight monitoring, if not repression, on the part of the superiors to ensure compliance and elicit work motivation in subordinates.

In the past few centuries, the developed world has overcome the repressive societal conditions characteristic of hierarchical agricultural feudalism. It is not the place here to reconstruct the complex historical processes by which this has been accomplished.[12] It suffices at this point to recognize that the two fundamental mechanisms continue to be present, albeit in forms that are adapted to further transformations of the production technology and the changing

[12] A key role may be attributed to the Enlightenment in Europe. It encouraged broad, educated circles to question the traditional social model of domination and submission and the accompanying privileges of the feudal aristocracy (Jacob, 1997). The idea of the "social contract" presented by Hobbes' Leviathan is an expression of the growing pressure on the established authorities to seek legitimization for their status and to subscribe to constitutional rules constraining their power. It has been argued that the movement towards legally limiting both the extent of domination and submission benefitted from the specific competitive situation between feudal authorities in Europe (Berman, 1983).

character of what are now the productive groups. In the political domain of civil societies that affirm egalitarian ideals, the superior-subordinate relationship is now restrained to conform with the principles of constitutional, democratic governance. In the organizational domain, the relationship is reconciled with the freedom of contract and, thus, subjected to mutual agreement.

In this section, we focus more specifically on the role that the two types of mechanisms play in the organizational environment that has emerged from the rise of industrial manufacturing and the production of services in the modern economy. The various disguises not withstanding in which the mechanisms now appear, it is still possible to identify the basic features. On the one side, one can observe those of the informal, egalitarian mechanism that suits the pro-social elements of our inherited behavioral repertoire. On the other side, it is not difficult to recognize the features associated with the dominance-based mechanism relying on the template of superior and subordinate with its long cultural tradition - the fact not withstanding that it now comes in the civilized version based on voluntary contractual arrangements.[13]

In its modern guise within firm organizations, the informal, egalitarian type of coordination can be characterized as follows. It strongly relies on informal communication across a flat organizational hierarchy, usually in small organizations or organizational units with intense face-to-face interactions. The team character of the group is emphasized. The superiors avoid a dominating attitude, or use only subtle forms, toward organization members reporting to them. Their role is closer to that of pro-social leaders. They promote groups interests, negotiate compromises where group interests and organizational goals are in conflict, and try to build consensus regarding task assignments. Once consensus is reached, the group members are given significant discretion in pursuing the tasks assigned, as well as considerable responsibility over the eventual outcome. These arrangements facilitate the members' identification with the organization and its goals.

If tasks are assigned largely by consensus and the members have a high identification with their groups, their commitment and work effort are likely to be high. A high degree of self-

[13] Within modern organizations there are often several subgroups which are sufficiently self-contained to develop their own solution to the dual problem so that variants of the two types may even coexist within one organization. A striking example is the military, the paragon of a hierarchical organization. It is based on unconditional authority, if not a repressive dominance relation, along the chain of command. Yet, at the same time, the military regularly offers the most impressive examples for group solidarity and loyalty at the level of the single squad.

determination in pursuing their tasks stimulates both achievement motivation and creativity. This, in turn, leads to a high degree of intrinsic work motivation (Deci and Ryan, 1985).[14] A pro-social attitude emerges that is likely to induce organization members to take on responsibility and reduces the temptation to free-ride. Under the conditions of this mechanism of coordination and motivation, monitoring of members' performance can therefore be done at a level that economizes on organization managerial resources.

However, the productivity-enhancing potential of this mechanism hinges to a considerable extent on the informal, pro-social leadership skills of the seniors in the organization, or a subdivision of it. Successful negotiating and consensus-seeking in face-to-face interactions require communicativeness, persuasiveness, and persistence, as well as fairness and credibility. Also, good judgment in aligning task assignments and the work abilities of individual members of the organization is necessary to avoid frustrating their intrinsic motivation by overtaxing them. Related to this, sensitivity to achieving a balance between extrinsic and intrinsic motivation (without the latter crowding out the former) is required. Extrinsic motivational features of the organization members such as remuneration, qualification enhancement, and career advancement, need to be considered and dealt with on a fair basis. All these capabilities may be considered part of a good pro-social leadership.

In contrast, the mechanism of coordination and motivation that rests on the traditional superior-subordinate template can be characterized as follows. It is based on the principle of authority, now defined on a contractual basis, e.g. by a labor contract. It is thus formally accepted by the subordinates. The coordination problem is taken care of by formally assigning the competence and responsibility for giving orders to one, or few, organization members at each layer of the organizational hierarchy. This means that the superior-subordinate template is extended throughout the organizational hierarchy. Subordinate members are contractually obliged and expected to seriously pursue the received orders. In principle, the production process can thus be coordinated in a very detailed and coherent way, and in so far, this specific form of firm organization may have a competitive advantage.

[14] With a remuneration considered sufficiently "fair", a reasonable balance between extrinsic and intrinsic rewards can be accomplished. The organization members are then motivated to pursue the assigned tasks with a level of effort significantly higher than can be induced with extrinsic rewards alone (Osterloh and Frey, 2000).

Leadership actually practiced under this coordination mechanism can widely vary. At one extreme, an authoritarian style adopts a dominating attitude and expects strict compliance. In some firm organizations, the style mimics the chains of command of the military (Chandler, 1979). At the other extreme, a more collegial style appeals to team spirit, explains reasons for orders, and tries to persuade subordinates. Yet, giving detailed orders and a narrow corset of directives constraining the subordinates' actions are part of either style. This leaves little discretion to the subordinates pursuing the assigned task and, hence, induces less identification with the task than in the case of the informal, egalitarian mechanism.

On the motivational side, lack of identification with the assigned tasks creates little, if any, intrinsic work motivation. The motivation to perform must therefore be elicited more by extrinsic rewards – remuneration, status, power.[15] Moreover, such an incentive structure may appeal to opportunistic tendencies in the subordinates, given the ambivalent human behavior traits mentioned above. Work effort may be reduced wherever possible (like in the case of free-riding in a cooperative group). The size of the extrinsic reward must therefore be made dependent on the level of performance, e.g. by paying at a piece rate. To be able to do so, more or less intense monitoring of the subordinates' performance is required. This increasingly demands the time of superiors as the organization or organizational unit for which they are in charge grows larger.[16] Moreover, as mentioned in the previous section, an agency problem arises whenever performance cannot be unambiguously assessed. If this is the case, it is difficult to even sanction the likely reduction of work effort.

[15] Personal progress in the organizational hierarchy becomes a dominant motive for many of the subordinate organization members, as this brings more extrinsic rewards in terms of remuneration and personal power. The pursuit of the goals of the organization is, at best, of instrumental value in this agonistic endeavor. Coming from a somewhat different interpretation of the evolution of social behavior, Nicholson (2010) reaches a similar conclusion: the balance between cooperative and competitive behavior is strongly dependent on the organizational framework, as is the importance of (rivaling) individual goals and status considerations.

[16] In fact, under this mechanism keeping work motivation in a growing organization under control requires increasing managerial resources. If they cannot be made available, this limits the growth of the organization (Penrose, 1959). If they can be made available – usually coinciding with an increasingly more elaborate organizational hierarchy – these resources are withheld from other, more productive, activities. Administrative costs increase and lead to “managerial diseconomies of scale” (Mueller, 1972).

6. Implications for organizational growth

Features of social behavior that have been shaped early on in human phylogeny thus leave their footprints in modern firm organizations. Organizations can take advantage of them particularly in the case of the informal, egalitarian mechanism of coordination and motivation and the strong emotional, cooperative attachment to the group and the high intrinsic work motivation it is able to elicit. The proviso is, of course, that, concerning the ambivalent human behavior traits, the selfish, opportunistic impulses to free-ride on the group's productive efforts can be kept in check. An intrinsically motivated pursuit of organizational goals (rather than of one's own that may not always accord with the organizational goals) is likely to be supported by pro-social pre-adaptations only so long as the organization members do not come to regard free-riding as a rewarding strategy. It is of great importance therefore how senior leadership responds to cases of free-riding and what is conveyed about it through across the channels of intra-organizational, informal communication and opinion formation in such cases.

An over-reaction of the superiors to observed free-riding can put the informal, egalitarian culture of the group at risk, e.g., when excessively using repressive means. A strategy to avoid this risk could be to appeal instead to pro-social values and loyalty to the group (moral suasions). On the other hand, a response by the superiors that does not stop free-riding behavior would run the risk of inviting imitation and, hence, the propagation of free-riding in the group. In this dilemma, an attempt to mobilize the informal communication within the team for a collective moral aggression or suitable form of social ostracism, as in the early human groups, can be an effective solution. However, the possibility to organize social ostracism against free-riders through the means of informal opinion formation within the group presupposes sufficiently intense face-to-face interactions between superiors and the members of the group. The frequency and intensity of the interactions tends to decrease with a growing group size, as do the chances of persuading the group members. For this reason, the ambivalence of the innate behavioral dispositions tends to manifest itself more as opportunism and free-riding the larger the organization or the organizational unit has grown. Even an initially cooperative mode can then be destabilized and eventually break down if group size grows beyond the bounds that have been mentioned above for early human groups (Witt, 1998; Cordes et al., 2010).

In this light, it does not appear accidental that, in large organizations, the mechanism of coordination and motivation is rarely that of the informal, egalitarian type, at least not with respect to the organization as a whole. Instead, more often than not, it is the dominance-based, hierarchical type that can be found. Shifting from an informal, egalitarian type to the other one may, in fact, even be necessary when free-riding becomes endemic and intrinsic motivation disappears. In such a case, a mode in which detailed orders, intense regulations, and tight controls are implemented may be the only way of preventing the organization's productivity from plunging. This normally requires establishing a costly managerial hierarchy. Individual work effort of the subordinates must then be elicited exclusively by extrinsic rewards or threats of sanctions. At the same time, monitoring of individual performance becomes mandatory. Once it has been made, the transition from an informal, egalitarian mechanism to a dominance-based, hierarchical one is difficult to reverse with the same staff. Intrinsic motivation is usually irreversibly "crowded out" by extrinsic motivation (Deci, Koestner and Ryan 1999). Trust in leaders is lost after seeing them transform from pro-social into authoritarian superiors. The emotional attachment to, and identification with, the organization or organizational unit is destroyed.

In favorable cases, a large firm with a dominance-based, hierarchical mechanism of coordination and motivation can, by virtue of its sheer size, attain a market position in which returns to scale and scope can be realized. This may compensate, or even over-compensate, for growing organizational slack and the lack of motivation of its members. Yet, stagnation or even decline are a permanent threat wherever such firms have to compete in or against innovative industries. The bureaucratic procedures and hierarchical controls of the large organizations stifle the commitment and creativity of employees. For that reason, such organizations have to expend more resources to generate new products or technologies than competitors that can draw on the creative potential of an informal, egalitarian culture.

For organizational theory, the implication is the following. If it is considered desirable to not be restricted to a dominance-based, hierarchical mechanism of coordination and motivation when a firm grows, deliberately planned steps must be taken to retain the informal, egalitarian mechanism. The conditions fostering close face-to-face interactions of the small group must be upheld through appropriate organizational measures. This is not feasible for large organizations as a whole. It can be realized, however, in the respective subdivisions and departments, so long

as they are small enough to develop their own, cooperative culture and are given enough independence to do so. Furthermore, it is not sufficient for leadership to rely solely on authority conferred to them. Instead, leadership must be based on personal capabilities and skills that allow the leaders at their level of responsibility to exert pro-social dominance as discussed before. Coordination between divisions and departments, and along the hierarchy of large organizations, needs to be accomplished by keeping up a culture of close face-to-face interactions among the leaders and those reporting to them at each level of the hierarchy. Top managers have to conceive of themselves and the managers reporting to them as one group in which the mechanism of coordination and motivation is that of the informal, egalitarian type. As said, managers need to adopt the role of pro-social leaders among peers and promote group interests, negotiate compromises where group interests and organizational goals are in conflict, and seek consensus regarding task assignments.

Daft (2011, 382-383) and Finkle (2012) discuss the instructive example of Google, a firm organization that has successfully solved this problem. One main feature of Google's governance policy was to conserve the “garage flair” of its early days, to stick with flat hierarchies and teamwork and (partial) self-determination of work schedules including flexible work hours. Strong emphasis was set especially on identification with the firm and its goals. The “Googlers” were encouraged to participate in various social events and extensive communication between the departments. The deliberate coining of group binding and pro-social slogans as “don't be evil” served the same purpose. Apart from its economic success, Google has turned out to also be very successful in the human relations dimension: it was and is able to recruit top personnel and can regularly be found at the top of various rankings of the most desirable places to work.

Another often cited example of a firm organization that has pioneered an informal, rather egalitarian culture is Southwest Airlines (Gittell 2003). The company started as a Texas-based regional operator in 1971, but by the year 2004 had become one of the largest airlines in the US. It is the company that achieved the breakthrough for the low-cost air carrier business. Its business model focuses on organizational practices designed to speed-up turnaround processes on the ground to increase the number of flights per aircraft per unit of time. (While on the ground, aircrafts do not generate any revenues.) No less than twelve different services contribute to turnaround at each airport: pilots, ramp and baggage transfer agents, cargo agents, mechanics,

fuelers, aircraft cleaners and caterers, ticketing and gate agents, flight attendants, and operations agents. A fast turnaround requires the efficient interaction of all these subunits.

The founders of the company tried to accomplish this goal by fostering a specific model of behavior in each of the teams at the different airports. They emphasized shared goals, shared knowledge, and the importance of mutual respect in the relationships between top management and local staff on the ground, as well as between the different service groups operating on the ground. In essence, their concept aimed at creating a coherent group on the ground at each airport that shared, and was motivated by, a vision of collectively contributing to a common goal. They actively supported the propagation of that vision in intense face-to-face interactions on site. In interview-based hiring procedures, the company took care to screen applicants for cooperative attitudes. The employees were given continued training in which they were encouraged to learn about ground services other than their own. Supervisors were urged to adopt a coaching and counseling attitude in managing frontline staff. Mentoring and conflict management were actively supported and suggestions for improvement were encouraged and put on the agenda for internal discussions.

In line with the present interpretation, it can be argued that, at least in part, the successful growth of these two very different companies, Google and Southwest Airlines, was based in each case on a consistent corporate striving to maintain the ideal of an informal, rather egalitarian mechanism of coordination and motivation inside their organizations – despite the growing organization size. Both firm organizations are characterized by departmentalization, flat hierarchies, and pro-social leadership based on personal attitudes and professional capabilities. The resources needed to implement such an organizational structure are likely to be substantial. Running an organization with such features requires time consuming efforts devoted to consensus-building. It will make high demands on the personality of the leaders. They face the problem of coordinating the interactions of subunits toward a coherent organizational performance without resorting, at all organizational levels, to the traditional template of superior and subordinate and the corresponding mechanism of coordination and motivation. Nonetheless, as the success of the two firm organizations given as examples show, such an endeavor may be worthwhile.

7. Conclusions

This paper has traced the "phylogenetic footprints" that can be observed in human social behavior in the context of organizations. Modern firm organizations crucially hinge on the social behavior and work attitudes of their members. We have shown how these are influenced by innate behavior traits that have been fixed at the times of early humans living in small bands. Modern humans do show a great deal of plasticity in their social behavior due to cognitive and reinforcement learning by which they adjust to the particular conditions of their social environment. However, the adjustments start from, and are constrained by, pre-adaptations which can therefore be expected to leave their mark also in the behavior of the members of modern organizations. These organizations are groups, after all – albeit more complex and often bigger ones than those of the early bands.

The explanatory approach we have used to explore the relevance of the pre-adaptations for organizational life and for organizational designs draws on Wilson and Gowdy's (2013) evolutionary tool kit. In consequence, we focus on the functionality and emergence of phenomena that are a product of evolution. In this vein, we have outlined an explanation for the way in which groups – humans or non-humans – that serve a productive function have solved a dual problem. Independent of the particular historical time and context in which such groups operate, their members' productive activities must first be coordinated toward jointly accomplishing the group's productive purpose. Second, their members must be motivated – intrinsically or extrinsically by incentives and controls – to contribute at an adequate level of effort in pursuit of that goal.

The solution of the dual problem is essential for survival and the competitive position of groups. It is therefore likely that genetic and/or cultural adaptations favor groups with more effective solutions to the problem. We have discussed the emergence of two very different mechanisms by which group members have been coordinated and motivated under different historical production technologies. One is an informal egalitarian mechanism, the other a dominance-based, hierarchical one. We have outlined why it can be conjectured that the respective mechanisms have been functional under the specific conditions and therefore had adaptive value for the groups adopting them. We have explained, moreover, in which way the innate social behavior traits relate to the functionality and emergence of these mechanisms.

We have then discussed in what modern guise the two mechanisms re-appear in present-day organizations, particularly firm organizations, and what their continued existence implies for the firms' performance and competitive position. The different mechanisms have been argued to correspond to different pre-adaptations in human social behavior that affect, in particular, the style of leadership and the work motivation of the organization members. These behavioral pre-adaptations thus also leave their "phylogenetic footprints" in the form of constraints on organizational design and prevent switching between the two mechanisms at will. Finally, we have addressed the role of a key variable – organization size – for the two mechanisms. As was pointed out, an informal, egalitarian mechanism is contingent on a small group size. Consequently, when the size of the organization grows beyond a certain bound, special measures need to be taken if the intention is to keep that mechanism alive. This has interesting implications for organizational design that have been briefly explored.

References

Alexander, R.D., 1974. The evolution of social behavior. Annual Review of Ecological Systems 5, 325-383.

Baker, M.C., Belcher, C.S., Deutsch, L.C., Sherman, G.L., Thompson, D.B., 1981. Foraging success in junco flocks and the effects of social hierarchy. Animal Behaviour 29, 137-142.

Bell, A. V., Richerson, P. J., McElreath, R., 2009. Culture rather than genes provides greater scope for the evolution of large-scale human prosociality. Proceedings of the National Academy of Sciences 106, 17671-17674.

Bernhard, H., Fehr, E., Fischbacher, U., 2006. Group Affiliation and Altruistic Norm Enforcement. Nature 442, 912-915.

Berman, H.J., 1983. Law and Revolution. The Transformation of the Western Legal Tradition. Harvard University Press, Cambridge, MA.

Berreby, D., 2005. Us and Them: the Science of Identity. Chicago University Press, Chicago.

Bingham, P.M., 1999. Human Uniqueness: a General Theory. Quarterly Review of Biology 74, 133-169.

Boehm, C., 1989. Ambivalence and compromise in human nature. American Anthropologist 91, 921–939.

Boehm, C., 1993. Egalitarian behavior and reverse dominance hierarchy. Current Anthropology 34**,** 227–254.

Boehm, C., 2001. Hierarchy in the forest: The evolution of egalitarian behavior. Harvard Unversity Press, Cambridge, MA.

Boehm, C., 2012. Moral Origins: The Evolution of Virtue, Altruism and Shame. Basic Books, New York.

Boserup, E., 1965. The Conditions of Agricultural Growth – The Economics of Agrarian Change Under Population Pressure. Aldine, Chicago.

Bowles, S., 2011. Cultivation of cereals by the first farmers was not more productive than foraging. Proceedings of the National Academy of Science 108, 4760-4765.

Boyd, R., Richerson, P. J., 1992. Punishment allows the evolution of cooperation (or anything else) in sizable groups. Journal of Ethology and Sociobiology 13, 171-195.

Browne, K.R., 2006. Evolved sex differences and occupational choice. Journal of Organizational Behavior 27, 143-162.

Burnham, T., 2013. IN THIS ISSUE -- TO BE ADDED

Campbell, D. T., 1965. Ethnocentric and other altruistic motives. In: Levine, D. (Ed.), Nebraska Symposium on Motivation. University of Nebraska Press, Lincoln, 283 – 311.

Chandler, A.D., 1979. The Visible Hand: the Managerial Revolution in American Business. Harvard University Press, Cambridge, MA.

Colarelli, S.M., Spranger, J.L., Hechanova, R., 2006. Women, power, and sex composition in small groups: An evolutionary perspective. Journal of Organizational Behavior 27, 163-184.

Cohen, M.N., 1977. The Food Crisis in Prehistory: Overpopulation and the Origins of Agriculture. Yale University Press, New Haven.

Cordes, C., Richerson, P.J., Schwesinger, G., 2010. How corporate cultures coevolve with the business environment: The case of firm growth crises and industry evolution. Journal of Economic Behavior and Organization 76, 465-480.

Daft, R.C., 2011. Organization Theory and Design. South Western College Publishers, Boston.

Deci, E.L., Koestner, R., Ryan, R.M., 1999. A Meta-analytic Review of Experiments Examining the Effects of Extrinsic Rewards on Intrinsic Motivation. Psychological Bulletin, 125, 627-668.

Deci, E.L., Ryan, R.M., 1985. Intrinsic Motivation and Self-determination in Human Behavior. Plenum Press, New York.

Deutsch Salomon, S., Deutsch, Y., 2006. OCB as a handicap: An evolutionary psychology perspective. Journal of Organizational Behavior 27, 185-199.

Drescher, S., Engerman, S.L., (eds.) 1998. A Historical Guide to World Slavery . Oxford University Press, Oxford.

Dunbar, M. R., 1993. Coevolution of neocortical size, group size and language in humans. Behavioral and Brain Sciences 16, 681-694.

Eibl-Eibesfeldt, I., 1997. Die Biologie des menschlichen Verhaltens.3rd Ed., Seehamer Verlag, Weyarn.

Eibl-Eibesfeldt, I., 1970. Ethology: The Biology of Behavior. Holt, Rinehart & Winston, New York.

Erdal, D., Whiten, A., 1994. On Human egalitarianism: An evolutionary product of Machiavellian status escalation? Current Anthropology, 35, 175-183.

Fehr, E., Gächter S., 2000. Fairness and retaliation: The economics of reciprocity. Journal of

Economic Perspectives 14, 159-181.

Finkle, T.A., 2012. Corporate Entrepreneurship and Innovation in Silicon Valley: the Case of Google, Inc. Entrepreneurship Theory and Practice, 36, 863-887.

Fried, M.H., 1967. The evolution of political society. Random House, New York.

Gintis, H., 2013. The evolutionary roots of human hyper-cognition. Journal of Bioeconomics, forthcoming.

Gitell, J.H., 2003. The Southwest Airlines Way: Using the Power of Relationships to Achieve High Performance. McGraw-Hill, New York.

Gowdy, J., Krall, L., 2013. Agriculture and the Evolution of Human Ultra-sociality. Journal of Bioeconomics, forthcoming.

Harner, M.J., 1970. Population pressure and the social evolution of agriculturalists.
Southwestern Journal of Anthropology 26, 67-86

Henrich, J. P., Boyd, R., Camerer, C., Fehr, E., Gintis, H., 2004. Foundations of Human Sociality: Economic Experiments and Ethnographic Evidence from Fifteen Small-scale Societies. Oxford University Press, Oxford.

Hill, K.R., Walker R.S., Bozicevic, M., Eder, J., Headland, T., Hewlett, B., Hurtado, A.M., 2011. Co-residence Patterns in Hunter-Gatherer Societies Show Unique Human Social Structure. Science 331, 1286-1289.

Hölldobler, B., Wilson, E.O., 2008. The Superorganism: The Beauty, Elegance,and Strangeness of Insect Societies. Norton, New York.

Hrdy, S., 1999. Mother Nature. Pantheon, New York.

Jacob, M., 1997. Scientific Culture and the Making of the Industrial West. Oxford University Press, Oxford.

Jones, E.L., 1993. Growth Recurring - Economic Change and the World History. Clarendon Press, Oxford.

Marlowe, F. W., 2005. Hunter-gatherers and human evolution. Evolutionary Anthropology: Issues, News, and Reviews, 14, 54-67.

Marshall, A., 1890. Principles of Economics. MacMillan, London.

Masters, R.D., 1989. The Nature of Politics. Yale University Press, New Haven.

Mueller, D.C., 1972. A life cycle theory of the firm. Journal of Industrial Economics 20, 199-219.

Nicholson, N., 2010. The design of work - an evolutionary perspective. Journal of Organizational Behavior 31, 422-431.

O'Riain, M.J., Faulkes, C. G., 2008. African mole rats: eusociality, relatedness and ecological constraints. In: Korb, J., Heinze, J. (Eds.), Ecology of Social Evolution, Springer, Berlin, 207-223.

Osterloh, M., Frey, B.S., 2000. Motivation, knowledge transfer, and organizational forms, Organization Science 11, 538-550.

Penrose. E.T., 1959. The Theory of the Growth of the Firm. Basil Blackwell, Oxford.

Quinn, R.E., Cameron, K., 1983. Organizational life cycles and shifting criteria of effectiveness: some preliminary evidence. Management Science 29, 33-51.

Riss, D., Goodall, J., 1977. The recent rise to the alpha-rank in a population of free-living chimpanzees. Folia Primatologica 27(2), 134-151.

Richerson, P.J., Boyd, R., 2005. Not By the Genes Alone – How Culture Transformed Human Evolution. University of Chicago Press, Chicago.

Sappington, D.E.M., 1991. Incentives in principal-agent relationships. Journal of Economic Perspectives 5, 45-66.

Seeley, T.D., 2010. The Wisdom of the Hive: The Social Physiology of Honey Bee Colonies, Harvard University Press, Cambridge, MA.

Sober, E., Wilson D.S., 1998. Unto Others: The Evolution and Psychology of Unselfish Behavior. Harvard University Press, Cambridge, MA.

Stiner, M.C., Barkai, R., Gopher, A., 2002. Cooperative hunting and meat sharing. Journal of Archeological Research 10, 1-63.

Van Vugt, M., Ahuja, A., 2010. Naturally Selected: The Evolutionary Science of Leadership. Harper, New York.

Van Vugt, M., Hogan, R., Kaiser, R., 2008. Leadership, followership, and evolution: Some lessons from the past. American Psychologist, 63, 182-196.

Wenzel, J.W., 1992. Behavioral homology and phylogeny. Annual Review of Ecology and Systematics 23, 361-381.

Werner, D., Flowers, N.M., Lattman Ritter, M., Gross, D.R., 1979. Subsistence productivity and hunting effort in native South America. Human Ecology 7, 303-315.

Wilson, D.S., 2002. Darwin's Cathedral: Evolution, Religion and the Nature of Society, University of Chicago Press, Chicago.

Wilson, D.S., 2011. Instant Expert: Evolution of Selfless Behavior, New Scientist, doi:10.101

Wilson, D.S., Gowdy, J., 2013. Evolution as a general theoretical framework for economics and public policy. Journal of Economic Behavior and Organization, this issue.

Wilson, E.O., 2012. The Social Conquest of Earth. Norton, New York.

Witt, U., 1998. Imagination and leadership – the neglected dimension of an evolutionary theory of the firm. Journal of Economic Behavior and Organization 35, 161-177.

Witt, U., 2005. The evolutionary perspective on organizational change and the theory of the firm. In: Dopfer, K., (Ed.), The Evolutionary Foundations of Economics. Cambridge University Press, Cambridge, UK, 339-364.

Witt, U., 2008. Observational learning, group selection, and societal evolution. Journal of Institutional Economics 4, 1-24.